DIRECTORY OF FUNCTIONS

Function	Brodmann's Areas
Motor	
Primary motor	4, 1, 2, 3
Secondary motor	6, 8
Motor planning	6, 13-16; 24, 32-33; 40
Motor Imagery	5, 7, 4, 6, 8; 24, 32-33
Motor Learning	4, 1-3, 6, 8; 23, 26, 29-31
Saccadic movements	4, 5, 7, 6, 8, 17, 18, 19, 46
Inhibition of blinking	4
Sensory	
Proprioception	1-3, 4, 8
Touch, temperature, vibration	1-3, 4, 5, 7, 13-16
Somatosensory integration	40
Auditory	
Basic processing	41, 42
Complex sounds processing	21, 22
Auditory Imagery	8, 9, 10
Familiar voices	38,
Visual	
Light intensity / patterns	17, 18, 19
Color discrimination	17
Visual integration	20
Visual motion processing	37
Olfaction	
General olfaction	11
Familiar odors	9, 10; 24, 32-33; 44, 45, 47
Language	
Comprehension	22, 20, 21, 37, 39, 40, 5, 7, 6, 9, 10, 23, 26, 29-31, 38, 43, 44, 45,47
Expression	44, 45, 46, 6, 8, 9, 10, 13-16, 21; 24, 32-33; 47
Prosody comprehension	22,
Reading	6, 39

Writing	40

Memory	
Working Memory	5, 7, 6, 8, 9, 10, 20; 24, 32-33; 40, 41, 44, 45, 46, 47; (27-28, 34-36, 48)
Episodic memory	6, 44, 45, 47
Retrieval	8, 9, 10,; 26, 29, 29-31; 24, 32-33; 38, 40,
Encoding	(27-28, 34-36, 48); 9, 10; 24, 32-33; 37, 46
Topokinetic	23, 26, 29-31

Attention	
Visual	17, 18, 37
Visuomotor	5, 7, 6, 8
Visuospatial	6, 8; 39, 24, 32-33; 45
Selective to sounds	6, 9, 10,; 24, 32-33
To speech	20, 22,; 23, 26, 29-31; 38, 47

Executive	
Planning	6, 8, 9, 10
Behavioral inhibition	6, 8, 9, 10, 13-16; 24, 32-33; 39, 40, 44 , 46, 47
Motor inhibition	24, 32-33, 44, 45, 47

Emotion	
Experiencing / processing emotion	38, 46; (27-28, 34-36, 48)
Related to language	23, 26, 29-31; 25,
Emotional stimuli	9, 10; 24, 32-33
Fear response	13-16

Pain	
Pain processing	13-16; 24, 32-33, 5, 7

Others	
Calculation	39, 40, 6, 8, 9, 10, 13-16, 46
Theory of mind	38, 9, 10, 20, 21, 22, 37, 47
Face recognition	37
Mental time-keeping	24, 32-33
Sexual arousal	24, 32-33
Humor comprehension	38
Music performance	40

Music enjoyment	44, 45, 46
Navigational skills	(27-28, 34-36, 48)
Novelty discrimination	(27-28, 34-36, 48)

Brodmann's Interactive Atlas

AREAS 1, 2 & 3

(Primary somatosensory cortex - Postcentral gyrus)

Associated Functions

- Somatosensory
  - Localization of touch (15488396, 11311865, 10841363, 9507956, many articles)
  - Localization of temperature (8836245, 16112876, 17689575, 10493903, many articles)
  - Localization of vibration (17065253, 16884928, 15019713, 10694461)
  - Localization of pain (18573266, 17512615, 15325369, 10493903)
  - Finger proprioception (17911031, 7807222, 11313298, more articles)
  - Deep proprioception (3a) (8891653)
  - Voluntary hand movement (12775191)
  - Volitional swallowing (10200226, 11568539, 10499047)
  - Tongue movement and perception (3 contralateral) (9347937)
  - Skillful coordinated orofacial movement (i.e. whistling) (16084116)
- Other
  - Somatosensory mirror neuron system (18345991, 18353686)
  - Pain anticipation (2, 3) (16704087)
  - Touch anticipation (i.e. tickling) (10936920)
  - Mirror neurons for speech perception (15734345)
  - Motor learning (11110829)

Reviewer's note:

The primary somatosensory area (SI) traditionally has been related with somatosensory perception (localization of touch, two-point discrimination, propioception, etc). Functional studies have demonstrated that SI also participates in movement organization (e.g., voluntary hand and tongue movements), “anticipation”, and “mirror neurons” (i.e., neurons that are active when observing the action of others). Mirror neurons were initially observed in macaques in the premotor and parietal cortical areas, and only recently, reported in humans. Mirror neurons probably play a crucial role in action understanding, anticipation, imitation, imagery, social behavior, and the like; that is, in the internal representations of actions. SI activation during movement performance reflects its participation in an extensive movement network that usually includes not only the primary motor cortex, but also the premotor cortex, the basal ganglia and the cerebellum.

AREA 4

(Primary motor cortex - Precentral gyrus)

Associated Functions

- Motor
  - Contralateral finger, hand, and wrist movements (Dorsal) (8643131, 8280976, 9343992, 10841363, 18486490, 18344193, many articles)
  - Contralateral lip, tongue, face, and mouth movement (Lateral) (9347937, 15162913, 15734345, 12599281, 11004117, 17560128)
  - Swallowing / laryngial movement (10200226, 11568539, 10499047, 17652461, many articles)
  - Contralateral lower limb (knee, ankle, foot, toe) movement (Mesial) (17919932, 16859927, 16034570, many articles)
  - Motor imagery (8922425, 18425505, 18358742, 17499160, many articles)
  - Learning motor sequences (15955490, 15585904, 11244547)
  - Volitional breathing control (11252531, 8350282, 10470862, 15311350)
  - Control of rhythmic motor tasks (i.e. bicycling) (11104128)
  - Inhibition of blinking / voluntary blinking (15882784, 12667852)
  - Horizontal saccadic eye movements (9345475, 9749761, 8492144)
- Somatosensory
  - Kinesthetic perception of limb movements (14987450, 14505336, 12467600)
  - Vibrotactile frequency discrimination (17065253, 10694461)
  - Finger proprioception (17911031, 7807222, 15029467)
  - Thermal hyperalgesia (contralateral) (8836245)
  - Response to touch/observed touch (Left) (18345991)
- Other
  - Verbal encoding during a non-semantic process (Right) (11338201)
  - Attention to action (posterior) (12091573)
  - Topographic memory (motor memory) for visual landmarks (9368932)

Reviwer's note

According to functional neuroimaging techniques BA4 participates in three different groups of functions: Motor, somatosensory, and “others” (“verbal encoding during a non-semantic process”, “attention to action”, and “motor memory for visual landmarks”). Motor function is the traditional function, and occasionally it has been reported that the primary motor cortex reacts to sensory stimulation. Nonetheless, in these cases the primary motor activation is found in addition to a more extensive pattern of activation, obviously including sensory areas; that is, the BA4 may some times be included in a brain circuitry supporting sensory perception; BA4 activation may reflect in those cases the implicit representation of a potential movement. This implicit representation of movements can also account for “attention to action” and “motor memory”. The participation in “verbal encoding during a non-semantic process” is probably tangential, considering that it becomes activated (in addition to frontal and temporal networks) only during “successful encoding”, suggesting a certain role in the attentional process (increased muscle tone?)

AREAS 5 & 7

(Secondary sensorimotor cortex - Secondary association sensorimotor cortex)
(Superior parietal lobule)

Associated Functions

Visuospatial processing (many articles) (mainly right 7)

- Mental rotation (16678867, 10611121)
- Stereopsis (11447346, 11997709)
- Perception of personal space (16162829, 17897686)
- Line bisection judgments (18249421)
- Processing chaotic patterns (18074783)
- Using spatial imagery in deductive reasoning (11958963)

- Motor
  - Motor imagery (7714579, 15166100, 12498743, many articles)
  - Processing tool-use gestures (Left) (15305134, 11545470)
  - Motor execution (7714579)
  - Mirror neurons (15091346)
  - Bimanual manipulation (18003884, 125270099)
  - Saccadic eye movement (11285015, 12595178, 9749761)
- Memory
  - Working memory (motor, visual, auditory, emotional, verbal) (9549504, 15204056, 11352614, 11240107, many articles)
  - Visuospatial memory (Right) (10666552)
  - Conscious recollection of previously experienced events (7) (8134341)
- Sensory
  - Tactile localization ("where stream") (15808973)
  - Pain perception (10368412)
- Attention
  - Visuomotor attention (16236528, 11784443)
- Language
  - Language processing (15449358)
  - Literal sentence comprehension (7) (17662699)
  - Word comprehension (imageability) (16716387)
  - Attention to phonological relations (7) (12457755)
- Other
  - Processing emotions and self-reflections during decision making (7) (15746230)
  - Goal-intensive processing (7) (11880658)
  - Temporal context recognition (Left 7) (8981471)

Reviewer's note Areas 5 & 7

The superior parietal lobe includes BA5 and B7, and is separated from the inferior parietal lobe (BA40 and BA39) by the intraparietal sulcus. The right secondary sensorimotor cortex is clearly involved in visuospatial processing, including the perception of the personal space and spatial imagery. Clinical observation demonstrates that the damage in the left superior parietal lobe is associated with ideomotor apraxia (loss of the ability to produce purposeful, skilled movements as the result of brain pathology not caused by weakness, paralysis, lack of coordination, or sensory loss). It is understandable that the secondary sensorimotor cortex participates in processing tool-use gestures,

motor imagery, bimanual manipulation, and similar praxic abilities. BA5/7 may also participate in a circuit underlying imitation of motor learning. It is well established that astereognosis (or tactile agnosia: loss of the ability to recognize objects by handling them) is found in cases of damage in the association sensorimotor cortex. Functional studies confirm that the superior parietal lobe participates in tactile localization whereas the inferior parietal lobe may be involved in tactile recognition. The superior parietal lobe also seems to participate in other processes, such as rhyme detection and semantic categorization tasks; and, interestingly, temporal context recognition.

AREA 6

(Premotor cortex or Lateral Premotor Area (PMA))
(Also includes Supplementary Motor Area (SMA))

Associated Functions

- Motor
  - Motor sequencing/planning (9549504, 15006042, 12202080, 11095535, 11240114, 10506098, many articles)
  - Motor learning (SMA) (15249112, 10806036, 10706432, 9827775, many articles)
  - Movement preparation/imagined movement (Rostral SMA) (10825359, 7714579, 7714579, 2263816, many articles)
  - Movement initiation (Caudal SMA) (10825359)
  - Motor imagery (SMA) (12731103, 12377173, 10554992)
  - Volitional control of breathing (11252531, 10523407, 8889766)
  - Horizontal saccadic eye movements (9345475, 8642414, 8595189)
  - Laughter/smiling (SMA) (12377151)
  - Interlimb coordination (10998121)
- Language
  - Speech motor programming (Left) (15766765, 11004117)
  - Language processing (SMA) (17524589, 17292926)
  - Language switching (10581218)
  - Reading novel words (aloud and silently) (Left) (15934062)
  - Speech perception (15184903, 8643761)
  - Updating verbal information (Medial) (15647494)
  - Phonological processing (Left) (12457755)
  - Object naming (Left) (11371315, 10484818)
  - Lipreading (SMA) (12750414)
  - Word retrieval (8624678)
  - Lexical decision on words and pseudowords (7820564)
  - Syntactical processing (?) (9831471)

- Memory
  - Working memory (12457762, 11352614, 10674479, 8134341)
  - Mnemonic rehearsal (8957565, 9345477)
  - Episodic long-term memory (12457762)

    - Topographic memory (9368932)
- Attention
    - Visuospatial attention (9126062, 7472342, 11467902)
    - Visuomotor attention (7472342)
    - Response to visual presentation of letters and pseudoletters (16154456, 12948705 (Left))
    - Updating spatial information (Lateral) (15647494)
    - Visual guided eye movements (frontal eye fields) (9212283)
    - Selective attention to rhythm/processing sequential sounds (Left) (9117371)
    - Attention to human voices (16340161)
- Other
    - Observation of actions (Mirror neurons) (12527103, 18450480, 16197695, 18539253)
    - Planning/solving novel problems (11880658, 10617267)
    - Executive control of behavior (11247659)
    - Reponse to baroreceptor stimulation (12077933, 11711862)
    - Generating melodic phrases (16817882)
    - Deductive reasoning (Left) (17904384, 11958963)
    - Response to strong odorant (Right) (17658690)
    - Formation of qualatative representations (16337816)
    - Processing emotions and self-reflections in decision making (Left) (15746230)
    - Same-different discrimination (Right) (11371315)
    - Calculation (11371315, 8740216)
    - Temporal context recognition (8981471)
    - Frequency deviant detection (9038285)

Reviewer's note Area 6

The diversity of functions involving BA6, probably the largest Brodmann's area, is not surprising. However, its basic function seems to be clear enough: motor sequencing and planning movements. Damage in the lateral premotor area results in kinetic apraxia (loss of the kinetic components of engrams resulting in coarse or unrefined movements with movements that no longer have the appearance of being practiced over time). The SMA portion is related with movement initiation. The left SMA also participates in language initiation and maintenance of voluntary speech production; but, interestingly, it also activates with imagined movements. Linguistic functions of left BA6 are diverse, but a major function evidently is speech motor programming; Broca's area indeed corresponds to a subdivision of the premotor cortex, and some of the linguistic functions of the lateral premotor area are probable the result of an extended activation of the frontal languages areas. By the same token, participation of BA6 in memory, attention, and executive functions may be due to the activation of an extended brain network, that sometimes involves BA6. The existence of mirrors neurons that activate when observing (and imagining) actions plays an important role in understanding thinking and planning.

AREA 8

(Part of prefrontal cortex - Lateral and medial supplementary motor area (SMA))

Associated Functions

- Motor
  - Motor learning (SMA) (15249112, 10806036, 10706432, many articles)
  - Motor imagery (SMA) (12731103, 10554992)
  - Motor control (10716244, 10599861)
  - Horizontal saccadic eye movements (8741338, 7953589)
  - Laughter/smiling (SMA) (12377151)
- Executive functions
  - Executive control of behavior (16859418, 11247659, 9674793, many articles)
  - Planning (10617267, 11810147)
- Language
  - Speech motor programming (Left) (11004117)
  - Language processing (SMA) (17524589)
  - Language translation (10581218)
  - Generating sentences (16817882)
  - Lipreading (SMA) (12750414)
- Memory
  - Working memory (11352614, 15833592, 10674479)
  - Perceptual priming (16701731)
  - Memory retrieval (Right) (9010011, 8551361)
  - Topographic memory (9368932)
- Attention
  - Visuospatial and visuomotor attention (7472342)
- Other
  - Sequence learning (12601101, 9801380)
  - Response to proprioceptive stimulation (12077933, 11711862, 11889505)
  - Pain anticipation (16704087)
  - Processing related to uncertainty (15006651)
  - Inductive reasoning (Left) (9175134)
  - Calculation (8904747, 8740216)
  - Auditory imagery (SMA) (11458829)

Reviewer's note

Traditionally BA8 has been regarded as the “frontal eye field”. However, functional studies report the participation of BA8 in a wide diversity of functions, including: motor, language, executive functions, memory, and attention. Only two studies refer to its participation in eye movements (horizontal saccadic eye movements). It is very interesting to note the participation of SMA in motor learning, supported by several studies. Usually it is accepted that SMA participates in initiating, maintaining, coordinating and planning complex sequences of movements performed in a particular order. Stimulation of the left SMA has been related to arrest of speech, and its damage to a particular type of language disorder referred as the “aphasia of the SMA” (initial mutism lasting about 2-10 days; virtually total inability to initiate speech; nearly normal speech repetition; normal language understanding; and absence of echolalia). The participation of BA8 in different executive functions (e.g., executive control of behavior, inductive reasoning, and planning) seems evident. BA8 also participates in memory processes, particularly in working memory. Its participation in sequence learning seems evident, but its involvement in response to proprioceptive stimulation, pain anticipation and auditory imagery does not seem so obvious; however, in auditory imagery, the activation of SMA may include rehearsal that involves motor programs.

AREAS 9 & 10

(Part of the prefrontal cortex - Middle frontal gyrus)

Associated Functions

- Memory
  - Working memory (14642465, 11960021, 11798278, many articles)
  - Spatial memory (16516248, 12126506)
  - Short-term memory (9) (15833592)
  - Memory encoding and recognition (12457762, 9010011, 10088902, many articles)
  - Memory retrieval (8134341, 11346889, 9010011, many articles)
  - Recency judgments (9) (8981471)
  - Event- and time-based prospective memory (10) (17126435)
  - Prospective memory (Lateral 10) (12667527)
  - Intentional forgetting (10) (17617657)
- Motor
  - Executive control of behavior (9) (16859418)
- Language
  - Syntactic processing (Left) (18255103)
  - Metaphor comprehension (Left) (17662699)
  - Verbal fluency (Left) (9) (12953304)
  - Semantic categorization (Left 9) (10495195)
  - Word-stem completion (Left) (9626676)
  - Generating sentences (Left 9) (16817882)
  - Verb generation (Left 10) (8592204)
- Auditory
  - Nonspeech processing (monaural stimulus) (10) (12062754)
- Other
  - Error processing/detection (9) (17274022)
  - Attention to human voices (9) (16340161)
  - Processing emotional stimuli (16317710)
  - Processing emotions and self-reflections in decision making (Left) (15746230)
  - Inferential reasoning (9) (8541472, 11958963, 9175134)
  - Decision making (involving conflict and reward) (Right 10) (10516320)
  - Planning (Right 9) (11880658)
  - Calculation / numerical processes (12914254, 10678698)
  - Attribution of intention to others (9) (10679187)
  - Intention/sensory feedback conflict detection (9) (10094258)
  - Smelling familiar odors (Right) (9950717)
  - Pleasant and unpleasant emotions (9352521)
  - Response to painful thermal stimuli (10) (9696465)
  - Joint attention (10) (15734350)

Reviewer's note-Areas 9 & 10

Without question, BA9/10 has a significant participation in memory, particularly memory encoding, memory retrieval, and working memory. Those studies relating BA10 with “event- and time-based prospective memory” and “intentional forgetting”, suggest the involvement of BA10 in controlling, and manipulating memory (metamemory). Hence, it could be argued that the middle frontal gyrus participates in an extensivememory circuit, and it has some fundamental role in organizing memory strategies and controlling memory. BA9/10 have also other evident executive functions, such as “executive control of behavior”, “inferential reasoning”, and “decision making”. Its participation in complex language processes may suggest the use of verbal strategies in executive processing; in these cases (e.g., syntactic processing, metaphor comprehension, generating sentences, etc), an extensive network is activated, involving diverse language related areas. Interestingly, BA10 seems to be involved in attending to sensory stimulation (e.g., response to baroreceptor stimulation, response to painful thermal stimuli, and joint attention). Two studies related the middle frontal gyrus with processing emotions. This involvement may be related to making decisions about emotional stimuli.

AREA 11

(Gyrus rectus)

Associated Functions

- Olfaction (9950717, 17658690)
- Auditory
    - Nonspeech processing (monaural stimulus) (12062754)
- Other
    - Decision making involving reward (15327927, 10516320)
    - Face-name association (Left) (11257289)

Reviewers's note

From the clinical perspective it is usually assumed that BA11 (base of the frontal pole) is related with something that could be termed “personality integrity.” Personality changes observed in traumatic brain injury individuals are supposed to result from damage of this orbital frontal area. Of course, “personality” (i.e., style of behavior) is an extremely difficult concept to approach in fMRI experiments. Nonetheless, it could be conjectured that BA11 participate in some individual’s “style of reacting” or “emotional idiosyncratic style”. In the available fMRI reports there is some paucity in the analysis of the emotional components of behavior. Only one study partially approaches this question (“decision making involving reward”)

AREAS 13, 14, 15 & 16*

(Insular Cortex)

Associated Functions

- Somatosensory
  - Pain processing (17611034, 16342273, 15010112, many articles)
  - Visceral pain perception (15500514, 12611986)
  - Thermal processing (17689575, 16051437, **, many articles)
  - Touch processing (16529950, 12145636)
  - Vibratory processing (15381714)
- Olfaction and taste (15933393, 14622239, 10495443, many articles)
- Memory
  - Verbal memory (episodic, working, retrieval) (11352616, 11002354, 10659091, many articles)
- Motor
  - Integration of limb and field coordinates (9125463)
  - Motor planning (16928798)
  - Swallowing (11681303)
  - Processing vestibular information (12805122)
- Language
  - Phonological processing (Left) (16845597)
  - Semantic processing (Bilateral) (12507948, 11702561)
  - Supraliminal priming during letter strings reading (Left) (17101688)
  - Overt speech tasks (Left) (15172523, 15068914)
  - Speech gesture learning (Left) (15275937)
- Other
  - Expression of fear response (11276236, 17123557)
  - Error awareness (17185003)
  - Motivated reasoning (17069484)
  - Response to reward fluctuation in decision making (16596979)
  - Response to informative feedback (motivation/reward processing) (16490307)
  - Risk-taking in decision processing (12948701)
  - Inhibition within an emotional context (16480897)
  - Autonomic arousal when watching emotional content (12784931)
  - Making emotional judgments (Right) (11467919)
  - Perceiving expressions of disgust (9333238)
  - Anticipatory deployment of attention in visual motion task (15275908)
  - Reproduction of nonlyrical tune (15068914)
  - Pitch judgment (8158246)
  - Executive processing (15053955)
  - Humor appreciation (15006673)
  - Strategy change response (14670576)
  - Calculation (11034863)

*These areas were not included in Brodmann's original map of the human brain, but are analagous to the location of the monkey's insular cortex.

Reviewer's note Areas 13,14,15 &16

The insula represents one of the most interesting and under-studied cortical areas. From the cytoarchitectonic point of view, it is quite heterogeneous: agranular in the anterior part and granular in the posterior region. It receives information from the ventral medial nucleus of the thalamus, the ventral posterior inferior nucleus of the thalamus, and the central nucleus of the amygdala. Reciprocal connections exist between the primary somatosensory cortex and the insula. The wide diversity of functions observed with fMRI studies (pain, temperature, touch, olfaction, taste, language, memory, emotion, etc) emphasizes its tremendous heterogeneity. Evidently, further research is required to pinpoint the participation of different insula areas in so diverse brain networks. fMRI studies have significantly contributed and continue contributing to our understanding of the insula functions.

AREA 17

(Primary visual cortex - Striate cortex)

Associated Functions

- Visual- Early visual processing
  - Detection of light intensity (12667837, 10997579, 9535979, 9543413, more articles)
  - Detection of patterns (18074783, 9345542)
  - Contour perception (10583491, 16269096, 10906313)
  - Color discrimination (15054055, 12678646, 10355906)
  - Visual attention (16054845, 15193585, 17715196, 16971677, more articles)
  - Visuo-spatial information processing (Right) (18249421, 16815338)
  - Processing spatial orientation (11102809, 17640531, 16221748)
  - Tracking visual motion patterns (optokinetic stimulation) (17575279)
- Memory
  - Visual priming (16901520, 15156146, 16901520)
  - Word and face encoding (?) (11522964)
- Other
  - Horizontal saccadic eye movements (9345475)

Reviewer's note

Complete bilateral lesions of the occipital lobes produce cortical blindness, which is some times associated with unawareness or denial of blindness (Anton's syndrome). According to functional studies BA17 clearly participates in the detection of light intensity, color recognition, and the detection of visual patterns. It also participates in visuo-spatial information processing, tracking motion and visual attention. fMRI studies have disclosed its involvement in some unexpected functions, such as visual priming, and word and face encoding; however in the latter case it is just one of the steps in a widespread network, including the bilateral frontal (BA44/45), occipital (BA17/18/19) and fusiform gyri (BA37) as well as the right hippocampal formation. Interestingly, BA17 is activated not only with the physical presentation of visual information, but also in mental imagery tasks

AREA 18

(Secondary visual cortex - Middle occipital gyrus)

Associated Functions

- Visual
  - Detection of light intensity (9345542, 16398586)
  - Detection of patterns (18074783, 15528095)
  - Tracking visual motion patterns (optokinetic stimulation) (17575279)
  - Discrimination of finger gestures (11525324)
  - Sustained attention to color and shape (9497430)
  - Visuo-spatial information processing (Right) (18249421, 11997709, 11467902)
  - Feature-based attention (16753563)
  - Orientation-selective attention (16221748)
- Memory
  - Visual priming (16901520, 15156146)
  - Word and face encoding (?) (11522964)
- Language
  - Response to visual word form (Left) (15183402)
  - Confrontation naming (12953304)
- Other
  - Face-name association (Left) (11257289)
  - Horizontal saccadic eye movements (9345475)
  - Response to emotion/attention in visual processing (Right) (10468363, 18502045)
  - Visual mental imagery (Left) (9117371)

Reviewer's note

Damage in BA18/19 is associated with visual agnosia, which can have different manifestations (e.g., object agnosia, face agnosia, color agnosia, topographical agnosia, etc.). Functions observed in neuroimaging studies include no only the detection of basic visual parameters (e.g., detection of light intensity, feature attention, detection of patterns, etc.), but also the area's participation in the “confrontation naming circuitry” (confrontation naming activates BA18/19/37 plus the inferior frontal gyrus). Damage in the left may be associated with pure alexia. It is not surprising either its participation in “response to visual word form”. According to functional studies it also participates in other visual related functions such as visual priming and visual attention.

AREA 19

(Secondary visual cortex - Inferior occipital gyrus)

Associated Functions

- Visual
  - Detection of light intensity (9345542, 16398586)
  - Visuo-spatial information processing (Right) (18249421, 11997709)
  - Detection of patterns (18074783, 12880816)
  - Tracking visual motion patterns (17575279, 7807222, 11954059, 11081835)
  - Discrimination of finger gestures (11525324)
  - Sustained attention to color and shape (9497430)
  - Feature-based attention (16753563)
  - Orientation-selective attention (16221748)
- Memory
  - Visual priming (16901520)
  - Visual memory recognition (15156146)
  - Word and face encoding (?) (11522964)
  - Spatial working memory (10601740)
- Language
  - Processing phonological properties of words (word form?) (15934062)
  - Confrontation naming (12953304)
  - Sign language (9222174)
- Other
  - Face-name association (Right) (11257289)
  - Horizontal saccadic eye movements (9345475)
  - Visual mental imagery (11958963)
  - Inferential reasoning (Left) (8541472)
  - Visual mental imagery (Left) (9117371)

Reviewer's note

Several visual functions found in BA18 are also observed in BA19; or, more exactly, in several visual functions (e.g., detection of light intensity, feature attention, detection of patterns, etc.) BA18 and BA19 are simultaneously activated, suggesting that they participate in a common brain network. In some other visual functions (e.g., spatial working memory; “where is it?”, that is, stimulus localization) only BA19 is active. It is interesting to emphasize that, BA19 participates in some language related functions, in particular processing phonological properties of written words (fusiform gyrus), confrontation naming (BA18/19/37 plus the inferior frontal gyrus) and sign language (BA37/19).

AREA 20

(Inferior temporal, Fusiform and Parahippocampal gyri)

Associated Functions

- Language
  - Lexico-semantic processing (Left) (15200701, 14969780)
  - Metaphor comprehension (Left) (15268917)
  - Semantic ambiguity comprehension (Right) (17142061)
  - Language comprehension and production (Left) (10725191)
  - Selective attention to speech (Left) (15183402)
- Visual
  - Visual fixation (15548215)
  - Integration of visual elements into perceptual wholes (Right) (11931928)
- Memory
  - Dual working memory task processing (Right) (15204056)
- Other
  - Attribution of intentions to others (10679187)

Reviewer's note

Usually, BA 20 is not included as part of Wernicke's area. Indeed, different authors describe Wernicke's area in not completely coincidental way: some authors only include the posterior part of the superior temporal gyrus (BA22); some authors include the superior and middle temporal gyri; and there are authors that even includ the angular gyrus of the parietal lobe as part of Wernicke's area. Functional neuroimaging studies suggest, without question, that BA20 should also be considered as part of Wernicke's area. Left BA20 participation in language understanding and processing is evident: lexico-semantic processing, metaphor comprehension, language comprehension and production, and selective attention to speech. Additionally, BA20, as part of the fusiform gyrus, also participates in some types of visual processing: in the integration of visual elements into perceptual wholes (single objects). BA20 involvement in the "attribution of intentions" seems to be marginal.

AREA 21

(Multimodal posterior area - Middle temporal gyrus)

Associated Functions

- Language
  - Selective processing of text and speech (Left) (15183402, 14754865)
  - Semantic processing (Left) (11346889, 16575838, 12457755)
  - Prosodic integration (Right) (15670670, 16275138)
  - Sentence generation (Left) (16817882)
  - Word generation (Left) (9710491)
- Visual
  - Observation of motion (8891654)
- Auditory
  - Processing complex sounds (Both hemispheres) (10489865)
- Other
  - Attribution of intentions to others (10679187)
  - Deductive reasoning (Left) (9869705, 8541472)

Reviewer's note

A rather complex level of language processing is found in BA21 (e.g., selective processing of text and speech and semantic processing). It also participates together with BA22 in processing complex sounds. Its activation along with BA45 when observing motion (mirror neurons?) seems intriguing. In the "attribution of intentions to others" paradigm, a rather extensive activation was observed: BA9/17/18/19/20/21/22/37/38/47; activation of language areas may suggest a verbal mediation.

AREA 22

(Superior Temporal Gyrus - Part of Wernicke's area)

Associated Functions

- Receptive language (Many articles in general)
  - Auditory language processing (Left) (12771248, 9222174)
  - Semantic processing (Left) (12457755, 16575838)
  - Sentence generation (16817882)
  - Frequency deviant detection (12948697)
  - Internally-specified word generation (Left) (11371315)
- Language-related
  - Selective attention to speech (16340161)
  - Affective prosody comprehension (Right) (15670701)
  - Learning a tone-based second language (Left) (14614812)
  - Repeating words (7891885)

- Auditory
  - Nonverbal sounds processing (Right) (15204072)
  - Processing complex sounds (10489865)
  - Lexico-semantic access to melodic representations (Anterior) (9117371)
- Visual
  - Remembered saccades (Right) (7953589)
- Other
  - Attribution of intentions to others (10679187)
  - Deductive reasoning (9869705)

Reviewer's note Area 22

Damage of BA22 in the left hemisphere results in Wernicke's aphasia (language disorder characterized by fluent speech, paraphasias -wrongly produced words-, and language understanding defects). Wernicke's aphasia however, is quite variable, depending on the exact location and extent of the brain damage. The diversity of linguistic functions observed in functional studies reinforces its crucial role in language reception and processing. Sounds with complex spectral intensity and temporal structures (words, speech, music) activates spatially extensive associative auditory areas in both hemispheres (BA 21/22), but right BA22 plays the fundamental role in nonverbal sound processing. As it is an auditory association area, its activation during non-auditory related tasks seems intriguing, e.g., "remembered saccades"; however, it should be noted that "remembered saccades" activates an extensive network including the striate and extra-striate cortex, posterior parietal cortex, frontal eye fields, supplementary motor area, insula, cingulate, thalamus, midbrain, cerebellum and BA22; BA22 participation is thus quite tangential. "Deductive reasoning" activates a complex brain network including in the left BA21/22/32/37/45/46/47 (kind of "executive function circuitry"), emphasizing that reasoning is partially mediated by language.

AREAS 23, 26, 29, 30 & 31

(Posterior cingulate gyrus)

Associated Functions

- Language
  - Lexico-semantic processing (Left) (15200701, 10454134)
  - Processing semantic emotional information (Left) (16084739, 9287369)
  - Selective attention to speech (Left 30) (15183402)
  - Passively listening to different sentences (Left 30) (16568419)
- Memory
  - Topographic and topokinetic memory (9368932, 15050583, 15670693)
  - Episodic memory retrieval (10510193)
  - Voluntary and involuntary recall (23) (17913256)
  - Word and face encoding (Right 30) (11522964)
  - Proactive interference resolution (17904389)
  - False recall (16648457)

Motor

  - Learning a complex motor skill (12902389)
  - Control of self-determined finger movements (9831446)
- Somatosensory
  - Response to thermal stimuli (10332889)
- Visual
  - High-demand visual processing/discrimination (15275904)
- Other
  - Evaluative judgment (23/31) (11906238)
  - Precautionary reasoning (29/31) (15994098)
  - Fear conditioning (Left) (15823161)
  - Self/other distinction (15298786)
  - Response to classical conditioning (8742426)

Reviewer's note Areas 23,26,29,30&31

According to functional studies the posterior cingulate gyrus does not seem as directly involved in motor initiation as the anterior cingulate gyrus does, although it is active when learning a complex motor skill. The posterior cingulate gyrus is seemingly more frequently activated during language tasks (e.g., lexico-semantic processing) than its anterior segment, but its role in emotion is obvious (e.g., fear conditioning) as well as its participation in different types of memory (e.g., topographic memory, episodic memory, etc.). Indeed, the brain areas involved in emotion, mainly the limbic system, including the cingulate gyrus, are the very same areas involved in memory. This simply means that there is a close association between emotion/motivation and memory: only information that is significant from the emotional/motivational point of view is memorized. Emotionally neutral information is usually ignored.

AREAS 24, 32 & 33

(Anterior cingulate gyrus)

Associated Functions

- Cognition
  - Cognitive/motor inhibition (16376861, 18325582, 15993771, many articles)
  - Experiential processing / processing of emotional cues (9712681, 18633805, 15130591, many articles)
- Motor
  - Motor preparation/planning (15519761, 11068195, 12146659)
  - Motor imagery (18425505)
  - Response to vestibular and ocular motor stimulation (11160520, 9712010, 12805122)
- Somatosensory
  - Pain (endurance?) (9696465, 8978344, 8895232, many articles)
- Language
  - Verbal initiation and suppression (Right) (9106283)
  - Object-naming (Left) (18639870, 8720681)
  - Semantic and phonological verbal fluency (Left) (18578599)
- Memory

    - Working memory (15040547, 14642465, 15893942, many articles)
    - Memory retrieval (Right 32) (9010011, 7719132)
    - Episodic memory encoding (12445630)
    - Prospective memory (9774166)
    - Time-based memory (17126435)
- Attention
    - Visuospatial attention (9126062, 16307253, 14642485)
    - Selective attention (9343611)
    - Divided attention (16337110)
    - Auditory attention (16340161, 9592060)
- Other
    - Mental timekeeping (16944489, 16730754, 15283476, many articles)
    - Self-other overlap during social perception (Mirror neurons) (16337816, 16035037)
    - Processing familiar odors (9950717, 16414279, 10980035)
    - Deductive reasoning (9869705, 11958963)
    - Inductive reasoning (Left) (9175134)
    - Taste (9929649, 7820672)
    - Sexual arousal to visual stimuli (males) (16467858, 11098795)

Reviewer's note

The cingulate gyrus belongs to the limbic system and its participation in emotion is obvious. Anterior cingulate gyrus damage can be associated with mutism and akinesia. Contemporary fMRI studies support its involvement in emotion (e.g., experiential processing / processing of emotional cues, sexual arousal to visual stimuli, etc.) and also in motor organization (e.g., motor preparation/planning, cognitive/motor inhibition) and language initiative (e.g., verbal initiation and suppression). In addition, when using functional neuroimaging some unexpected BA24/32/33 functions are found, such as response to vestibular and ocular motor stimulation, executive functions (e.g., deductive reasoning, inductive reasoning, and mental timekeeping) and different types of memory (e.g., working memory, episodic memory, prospective memory, etc.)

AREA 25

(Subgenual gyrus)

Associated Functions

- Other
    - Evaluating emotional words (Left) (12454910, 10852235)
    - Implicit moral reasoning (16418007)
    - Mechanical hyperesthesia (15030948)

Reviewer's note Area 25

Regardless of the limited number of studies, it is extremely interesting to find that BA25 participants in clearly emotional/motivational executive functions, i.e., “evaluating emotional words”. BA25 seems to participate in processing of nociceptive information, also an emotional related function. Interestingly, BA25 is active during moral reasoning (a clearly executive function), in addition to other brain areas such as BA47 and BA6.

AREAS 27, 28, 34, 35, 36 & 48*

(Hippocampal areas - Part of medial temporal lobe)

Associated Functions

- Memory
  - Memory encoding (many articles)
    - Verbal-semantic (Left) (16831858, 16472901, 16725214, many articles)
    - Faces (17604351, 15927485, 12498747, many articles)
    - Picture (15927485, 10739366)
    - Auditory (15054061)
    - Emotional (14758364)
  - Working memory (many articles)
    - Verbal-semantic (16051547, 15884095, 17403529)
    - Visual (16949839)
  - Episodic memory (many articles)
    - Autobiographical (17548799, 17204823, 16518010, many articles)
    - Olfactory and gustatory (16414279, 16839610, 17951077, many articles)
  - Recognition memory / memory recall and retrieval (17696171, 17958471, 17993209, many articles)
  - Procedural memory consolidation (18439410, 18387582, 18155926, many articles)
  - Memory for novel/unexpected stimuli (anterior) (17354068)
  - Negative priming (18281155)
- Emotion
  - Memory for unpleasant/fearful emotional stimuli (amygdala-hippocampal junction) (17354068, 17290372, 16952466, many articles)
  - Facial emotional perception (12099486, 12169250, 11997687, many articles)
  - Processing disgust-inducing and erotic images (16038771, 15488301)
  - Experience and regulation of emotional stress (15677422)
  - Expressing congruent facial movements (mirror neurons) (12738341)
  - Craving (15589112)
  - Hunger (12079866)
  - Embarrassment (15528097)
- Navigational Skills
  - Spatial (18240326, 17924521, 17893237, many articles)
  - Contextual ("landmark retrieval") (parahippocampal) (18240326, 17893237, 15506871, many articles)
- Other
  - Novelty discrimination (12457753)
  - Past (right & left) and future (right) event construction (17126370)
  - Relational processing during elaboration of future events (18157862)
  - Anticipating regret (i.e. gambling) (16116457)
  - Insight in problem solving (12722972)
  - Informed decision-making (11927193)
  - Pattern separation (among common episodes) (17848502)

- Detection of deviant stimuli (15390157)

*Area 48 was described by Brodmann, but not placed on his original map of the human brain.

Reviewers note 27,28,34,35,36&48

Hippocampus damage results in severe anterograde amnesia associated with a partial (2-3 years) retrograde amnesia. This observation suggests a long-term consolidation process lasting 2-3 years. Hippocampal asymmetry has been established, and in cases of left hippocampal lesions amnesia is more language-related, whereas in cases of right damage, a more nonverbal amnesia is found. According to the brain functional imaging studies, the hippocampus participates in a wide variety of memory processes, including: working memory, semantic memory, episodic memory, and memory retrieval. Hippocampus becomes also active in some emotional conditions (e.g., disgust, unpleasant/fearful stimuli, facial emotional perception, etc.); in these last cases usually the amygdala and other brain structures are also involved. Interestingly, the hippocampus is also related with "novelty discrimination" and "detection of deviant stimuli". Some authors have even suggested that this is a primary function of the hippocampus: a kind of comparator that determines whether the current information is new (and should be stored in memory), or it is old (and no storage is necessary). The "anticipatory" function of the hippocampus reported in some studies, such as "anticipating regret", "relational processing during elaboration of future events" and "future event construction," is intriguing. In this anticipatory function prefrontal cortex is also involved, and hippocampal participation may suggest the use of memories as kind of templates used to anticipate future events.

AREA 37

(Posterior inferior temporal gyrus, middle temporal gyrus, and fusiform gyrus)

Associated Functions

- Language
  - Semantic categorization (Left) (15993766, 11099727)
  - Word retrieval (Left) (12953304)
  - Attention to semantic relations (Left) (12457755)
  - Word generation (Left) (9710491)
  - Sign language (9222174)
  - Single letter processing (Left) (15006649)
  - Metaphor comprehension (Left) (15268917)
  - Orthography-phonology link (Left) (15091345)
- Memory
  - True and false memory recognition (15156146)
  - Episodic encoding (11522964)
- Visual
  - Face recognition (mostly fusiform gyrus) (12880816, 15268916, 8126548)
  - Visual motion processing (11907693, 7807222, 11954059)
  - Visual fixation (15548215)
  - Structural judgments of familiar objects (15714895)
  - Sustained attention to color and shape (9497430)
- Other
  - Face-name association (Left) (11257289)

- Attribution of intentions to others (10679187)
- Deductive reasoning (Left) (9869705)
- Drawing (16944477)
- Motion aftereffect (10725183)

Reviewer's note Area 37

It is well known that BA37 is involved in lexico-semantic associations (i.e., associated words with visual percepts). Clinical observations have demonstrated that damage in the left BA37 usually results in word-finding difficulties and semantic paraphasias. Therefore, it is not unexpected that functional studies have found that left BA37 participates in semantic categorization, word retrieval, word generation, face-name association, and attention to semantic relations. Its participation in sign language is not unexpected either, as well as BA37 participation in some aspects of reading (e.g., single letter processing and orthography-phonology link), because visual-language associations are involved. The basal aspect of BA37 corresponds to the fusiform gyrus, which is indeed an extension of the visual association areas, and has visual functions. Hence, BA37 involvement in complex visual functions, such as face recognition, and structural judgment of familiar objects is not surprising. It is known that prosopagnosia (acquired inability to recognize faces) is the result of brain pathology involving the right fusiform gyrus (temporal-occipital) or both fusiform gyri. BA37 seems to be also participating in some memory circuitries, particularly when visual information is involved. In the experiments about "attribution of intentions" there is a complex pattern of brain activation, and BA37 involvement may be tangential. Deductive reasoning studies have shown a complex brain network responsible for this particular executive function, including BA21/22/24/32/37/45/46/47; BA37 activation (as well as the activation of other language-related areas) is simply supporting the linguistic underlying nature of the task. Disturbances in drawing (constructional apraxia, or simply visuoconstructive disorder) are observed in cases of right hemisphere pathology, and according to fMRI studies, drawing activates right BA37.

AREA 38

(Temporal pole)

Associated Functions

- Cognition
  - Attribution of intentions/mental states to others (10679187, 16687157, 16122944, many articles)
  - Self/other distinction (Left) (15298786, 16478667, 15784441)
  - Moral judgments (16768379, 12169253)
- Emotion
  - Experiencing emotional states (12821792, 12814585, 10459394)
  - Visual processing of emotional images (10468363, 14568451, 10355673, many articles)
  - Response to threat/fearful stimulus (18307211, 17270466)
  - Emotional attachment (16087352, 15257156)
- Memory
  - Multimodal memory retrieval (17622649, 10694462, 10985287, many articles)
- Language
  - Semantic processing (Left) (11906233, 11906232, 12126497, many articles)
  - Speech comprehension (Left) (14754865, 7820563)
  - Naming of items learned in early life (Left) (16987673)

    - Word retrieval for specific entities (Left) (11410949)
    - Lexico-semantic ambiguity processing (Left) (15884095)
    - Narrative comprehension (Left) (10506087, 9579674)
- Auditory
    - Selective attention to speech (Left) (15183402, 18053971)
    - Response to tone stimulus (12208550)
    - Response to aversive auditory stimulation (12169258)
    - Identification of familiar voices (Right) (11440757)
- Visual
    - Color and structural judgments of familiar objects (15714895)
- Other
    - Humor comprehension (17069470, 16275931)
    - Irony processing (Right) (17689103)
    - Inferential reasoning (Left) (8541472)
    - Pleasant response to music (17466401)

Reviewer's note Area 38

Functional studies have disclosed the unexpected complexity of BA38 functions. Because of its location in the brain, it is understandable that BA38 participates in language processes, emotion, executive functions, and memory. Left BA38 is involved in diverse “high level” verbal functions (e.g., semantic processing, naming of items learned in early life, lexico-semantic ambiguity processing, etc.). Departing from the reported functional studies BA38 involvement in emotion seems evident (e.g., visual processing of emotional images, emotional attachment, response to threat/fearful stimulus, etc.). In some executive functions (e.g., moral judgment, inferential reasoning, etc) BA38 is also active. Diverse studies support BA38 contribution to multimodal memory retrieval. Additionally, it seems to contribute to some complex auditory processing; for instance, recognition of familiar voices (phonognosis), and response to aversive auditory stimulation. Interestingly, traumatic head injury usually impacts the temporal pole, and it has been suggested that the difficulties to separate auditory “figure” (e.g., language) from background “noise” found in patients with head injury, is a result of BA38 damage.

AREA 39

(Part of inferior parietal lobule - Caudal bank of intraparietal sulcus - Angular gyrus)
(Part of Wernicke's area)

Associated Functions

- Language
    - Sentence generation (Left) (16817882)
    - Reading (9831471, 15200701)
- Calculation
    - Calculation (Left) (14585751, 17851092)
    - Arithmetic learning (Left) (14659499)
    - Abstract coding of numerical magnitude (Left) (17224409)
- Visual
    - Spatial focusing of attention (16860474)
    - Visuospatial processing (Right) (8547586)
- Other
    - Performingverbal creative tasks (Left) (15172131)

    - Theory of mind (8541472)
    - Executive control of behavior (16859418)
    - Processing a sequence of actions (Left) (10617267)
    - Sight reading (music) (Right) (12488812)

Reviewer's note Area 39

The angular gyrus is a cortical area involved in cross-modal association among somatosensory (body knowledge) information, auditory information and visual information. Developmentally, the angular gyrus is one of the last to functionally and anatomically maturate. Classically, it has been assumed that the left angular gyrus participates in calculation abilities, reading/writing, naming and some type of body-knowledge (somatognosis). The deficit associated to left angular lesion (Gertsmann's syndrome) includes acalculia, agraphia, r-l disorientation, and finger agnosia. Spatial knowledge mediated by language has been proposed as a basic underlying deficit observed in cases of L angular gyrus damage, responsible for observed acalculia, and so called sematic aphasia. fMRI studies support the role for angular gyrus in arithmetic abilities, but seemingly the really most crucial area in number processing is the intraparietal sulcus. BA39 activation is observed in some reading related tasks (understanding the relationship among different characters) but no reports are readily available about its participation in writing because writing may be more exactly associated with the superior parietal lobe and BA40 (apraxic agraphia in cases of parietal lobe damage). The R angular gyrus clearly participates in visuospatial process and damage to it results in severe hemi-spatial neglect. In addition BA 39 seems to participate in an executive function brain circuitry, and it activates in tasks such as verbal creativity, inferential reasoning and processing sequences.

AREA 40

(Inferior parietal lobule - Supramarginal gyrus)

Associated Functions

- Language
    - Attention to phonological relations (12457755)
    - Semantic processing (more elaborate and complete) (16575838)
    - Verbal creativity (15172131)
    - Writing of single letters(16506011)
- Memory
    - Retrieval of unpleasant experiences (18502045)
    - Working memory (emotional/auditory related) (11352614)
    - Conscious recollection of previously experienced events (8134341)
- Motor
    - Executive control of behavior (16859418)
    - Response to aversive stimuli (16162829)
    - Visually guided grasping (15820646)

    - Gesture imitation (15769494, 15305134)
    - Visuomotor transformation/motor planning (15062860)
    - Repetitive passive movements (10724112)
    - Intention/sensory feedback conflict detection (10094258)
- Somatosensory
    - Somatosensory spatial discrimination (18234508)
    - Integration of tactile and proprioceptive information (17451973)
- Visual
    - Response to visual motion (7807222)
- Other
    - Deductive reasoning (17904384, 11958963)
    - Social perception and empathy (16337816)
    - Emotions vs. self-reflections in decision-making (Right) (15746230)
    - Music performance processing (15062860)
    - Goal-intensive processing (11880658)
    - Same-different discrimination (Right) (11371315)
    - Calculation (integer computation) (Left) (11371315)
    - Motion after-effect (10725183)
    - Performing creative tasks (Left) (15172131)

Reviewer's note

The supramarginal gyrus of the left hemisphere appears to support some complex linguistic processes, such as semantic processing and verbal creativity. Its role in spatial knowledge, and particularly, controlling movements guided by visuospatial information seems evident. Its role in calculation is probably related with its adjacency to the angular gyrus and intraparietal sulcus. The left supramarginal gyrus seems to be involved in some complex motor activity, such as motor planning; this function is continued in the superior parietal lobe. BA40 also participates in an executive function network, involved in tasks such as deductive reasoning and performing creative tasks

AREAS 41 & 42

(Primary auditory cortex - Heschl's gyrus)

Associated Functions

- Auditory
    - Basic processing of auditory stimuli (speech and non-speech) (18367601, 18023460, 17851933, 15936503, 10489865, many articles)
    - Processing discontinued acoustic patterns (42) (10489865)
    - Frequency deviant detection (12948697)
    - Perception of harmonic tones (right > left) (11739262)
    - Processing sound intensity (12742243, 12703014)
    - Sensitivity to pitch (18044637, 12441063)
    - Rapid sound detection (Bilateral) (17175176)
    - Sound (vowel) segregation (15907316)
    - Auditory priming (8134341)
- Memory

    - Repetition priming effect (11247649)
    - Auditory working memory (12589893)
- Other
    - Visual speech perception (mirror neurons?) (12590843, 15671860)

Reviewer's note

The primary auditory area contains a frequency map: different neurons respond best to particular frequencies. This frequency distinction is also found in the cochlea and the auditory pathway to the brain. It means, that the primary auditory cortex possesses a tonotopic organization. Bilateral lesions of Heschl's gyri may result in central deafness. Heschl's gyrus involvement in basic processing of auditory stimuli, processing discontinued acoustic patterns, rapid sound detection, and similar auditory processes seems quite obvious. Its activation during visual word recognition and auditory short-term memory also seems understandable. Nonetheless, it may be unexpected and intriguing that it activates when reading speech from faces (watching articulatory gestures). This may suggest and internal representation of the speech sounds (mirror neurons?).

AREA 43
(Subcentral area)

Associated Functions

- Motor
    - Response to vibrotactile digit stimulation (10694461)
- Language
    - Spoken language (Bilateral) (9222174)

AREA 44
Broca's Area
(Inferior frontal gyrus - Pars opercularis)

Associated Functions

- Language (left hemisphere in majority of people) (Many articles, in general)
    - Semantic and phonological fluency (18296070, 12953304, 15109996)
    - Phonological or syntactic processing (12457755, 12668238, 10547332)
    - Grapheme-to-phoneme conversion (16310346, 11798383)
    - Grammatical processing (16881266)
    - Processing of sequential sounds (9117371)
    - Lexical inflection (Left) (16881266)
    - Response to unintelligible speech (16781167)

    - Expression of emotional information (Right) (15670701)
    - Perception of prosodic information (intonation) in speech (Right) (15670701, 15670670)
    - Attention in speech processing (14754865)
    - Sentence comprehension (11896643)
    - Internally-specified word generation (9710491)
- Memory
    - Syntactic working memory (15455462, 18255103)
    - Working memory (12457762, 11352614, 15862203)
    - Episodic long-term memory (12457762)
    - Declarative memory encoding (10088898)
- Motor
    - Mirror neurons for expressive movements (16730755, 16337816, 12527103)
    - Motor speech programming (15109996)
    - Motor response inhibition (Right) (19922390)
- Others
    - Generation of melodies (Right) (16817882)
    - Tactile imagery (12657890)
    - Goal-intensive processing (11880658)
    - Word and face encoding (11522964)
    - Solving arithmetical tasks (10678698)
    - Motion after-effect (10725183)
    - Object manipulation (bilateral) (10473761)
    - Smelling familiar odors (Left) (17951077, 15038008)
    - Music enjoyment (16078183)

Reviewer's note Area 44

From the traditional point of view, Broca's area corresponds to BA 44, but several contemporary authors also include BA 45. It can be conjectured that in the future, the most anterior part of the insula could also be included in the Broca's area, given its participation in the praxis of speech (motor speech programming). Different proposals have been presented to explain language disturbances in so-called Broca's aphasia; different hypotheses have attempted to postulate a core BA44 function, including: binding the elements of the language, selecting information among competing sources, generating/extracting action meanings; sequencing motor/expressive elements; cognitive control mechanism for the syntactic processing of sentences; construction of higher parts of the syntactic tree in speech production; and verbal working memory. Functional studies have further improved our understanding of BA44. Although the core BA44 function remain elusive, fluency and sequencing may potentially account for many of the functions in which BA44 participates. The suggestion that BA44 includes mirror neurons for expressive movements is particularly provocative and may enlighten the question of inner speech (e.g., internally generated language). Functional studies have also contributed to further understand right BA44, which seemingly participates in perception and expression of prosodic and emotional information. From the perspective of the lesional model, unfortunately just few studies have analyzed the clinical disturbances associated with right BA44. Functional studies have also disclosed the participation of BA44 in a diversity of tasks that are difficult to interpret with our current understanding of the brain, such as pain anticipation, perception of tactile stimulation, motion after-effect, object manipulation, smelling familiar odors, and music enjoyment; in those cases, BA44 activation is just an additional element in a complex brain network; it may be suggested that some internal verbalization can account for BA44 involvement in these unexpected activities. Its participation in working memory may also reflect the internal rehearsal of the information.

AREA 45
Broca's Area
(Inferior frontal gyrus - Pars triangularis)

Associated Functions

- Language (Many articles, in general)
  - Semantic > phonological processing (15647526, 15109996, 12457755, 10547332, 15109996)
  - Internally specified word generation (16990015, 9710491, 11371315, 10510191)
  - Verbal fluency (12953304, 9192679)
  - Lexical search (16310346; 11798383)
  - Phonological processing (12668238,11673166)
  - Grammatical processing (16881266)
  - Semantic memory retrieval (11346889,10547329, 16575838)
  - Selective attention to speech (Left) (15183402)
  - Sign language (14572520)
  - Affective prosody comprehension (Right) (15670701)
  - Lexical inflection (Left) (16881266)
  - Reasoning processes (9869705, 9175134)
  - Processing of metaphors (15268917, 17662699)
- Memory
  - Working memory (12457762, 11352614)
  - Non-verbal working memory (bilaterally) (15588614)
  - Episodic long-term memory (12457762)
  - Declarative memory encoding (10088898)
  - Recall of digit series (15862203)
- Motor
  - Mirror neurons for expressive movements (16730755)
  - Mirror neurons for grasping movements (8891654)
  - Response inhibition (Right > left: 16421886) (Left>Right:11467901) (bilat:11170305)
- Other
  - Mental rotation (mostly in females) (16678867)
  - Word and face encoding (11522964)
  - Aesthetic appreciation (16087351)
  - Music enjoyment (16078183)
  - Generation of melodic phrases (Left) (16817882)
  - Modulating emotional response (18002729)
  - Smelling familiar odors (Left) (17951077, 15038008)

Reviewer's note

Without question, the functions of BA45 are significatively coincidental with the functions of BA44, supporting the proposal that they both, at least partially, correspond to a single system. Nonetheless, BA45 seems to be involved in relatively more complex verbal functions, for instance, processing of metaphors and reasoning processes. As observed with BA44, BA45 participate in a diversity of functions difficult to interpret with our current understanding of the brain (e.g., smelling of familiar odors) and probably reflecting some inner speech during the performance of those tasks. BA45 participation in working memory may also reflect the internal rehearsal of the information.

AREA 46

(Part of the prefrontal cortex - Anterior middle frontal gyrus)

Associated Functions

- Memory
  - Memory encoding and recognition (12457762, 9010011, 8134340, many articles)
  - Working memory (14642465, 11960021, 12126506, many articles)
- Language
  - Semantic processing (Left) (7666172, 8957565, 18255103)
  - Verbal fluency (Left) (12953304, 8592204)
  - Phonological processing (Left) (12668238)
- Motor
  - Executive control of behavior (16859418)
  - Chewing (18403120)
  - Drawing (16944477)
  - Mirror neurons (15091346)
  - Horizontal saccadic eye movement (7953589)
- Other
  - Internal mental calculation (12914254, 8592209)
  - Processing emotions and self-reflections in decision making (Left) (15746230)
  - Intention/sensory feedback conflict detection (10094258)
  - Music enjoyment (16078183)
  - Willed action (1679944)
  - Strategy change response (14670576)

Reviewer's note

Departing from the neuroimaging studies it is evident that BA46, as well as BA9/10, is involved in memory, particularly working memory and memory control and organization. Because of the association of working memory with prefrontal activity, some clarification about working memory is important. It has been assumed that working memory is involved in a diversity of cognitive processes, including language comprehension, planning, reasoning, problem solving and even consciousness. It is important to emphasize that span tests (e.g., digit span) (working memory storage process) exhibit greater dependence on the posterior cortex, whereas delayed recognition performance (working memory rehearsal process) exhibits greater dependence on the prefrontal cortex. When information has to be manipulated, increased prefrontal activity is found. The manipulation-related processes ascribed to the dorsolateral prefrontal cortex are fundamentally extramnemonic in nature (that means, metamemory). Whereas they play a fundamental role in the exercise of executive control of working memory, they do not govern the storage per se of the information held in working memory. The participation of the left anterior middle frontal gyrus in language is also shared by other left prefrontal convexital areas; according to current knowledge of languages disturbances associated with brain pathology, other linguistic functions potentially related with BA46, such as verbal initiative and language pragmatics, have not been fully approached in fMRI studies. Two fMRI studies attract special attention: (1) “Willed acts” in the two response modalities studied (speaking a word, or lifting a finger) were associated with increased blood flow in BA46; (2) mirror neurons: a basic circuit underlying imitation learning including the inferior parietal lobule and the posterior part of the inferior frontal gyrus plus the adjacent premotor cortex (mirror neuron circuit) has been proposed. During pause, the middle frontal gyrus (area 46) plus those structures involved in motor preparation (dorsal premotor cortex, superior parietal lobule, rostral mesial areas) also become active.

AREA 47

(Inferior frontal gyrus - Pars orbitalis)

Associated Functions

- Language
  - Semantic processing (Left) (17524589, 16575838, 12062754)
  - Semantic encoding (11543056, 7666172)
  - Active semantic retrieval (15812317, 15528098, 8595473)
  - Phonological processing (17524589, 12457755)
  - Single word reading (16253527)
  - Lexical inflection (16881266)
  - Affective prosody (Right) (15670701)
  - Selective attention to speech (15183402)
- Memory
  - Working memory (12457762, 8134340)
  - Episodic long-term memory (12457762)
- Other
  - Behavioral and motor inhibition (Right) (16420462, 15827569)
  - Adverse emotional inhibition (12135962)
  - Nonspatial auditory processing (15110033)
  - Processing of fine-structured stimuli (i.e. music) (Left) (14683718)
  - Temporal coherence (language and music) (16516496)
  - Lexico-semantic access to melodic representations (9117371)
  - Smelling familiar odors (Left) (17951077, 15038008, 9950717)
  - Attribution of intention to others (10679187)
  - Decision making (involving conflict and reward) (Right) (10516320)
  - Deductive reasoning (9869705, 9175134)

Reviewer's note

The significant amount of language-related functions that have been associated with BA47, such as semantic processing, phonological processing, semantic encoding, and others, is surprising. In these cases, BA47 is simply one of the multiple steps in the brain language processing network. It could be further speculated that in these verbal related functions, the inferior frontal gyrus may play a more emotional/motivational function. Moreover, anatomically BA47 is adjacent to BA45, a clearly language brain area. BA47 participates in some clearly emotional related activities (e.g., adverse emotional inhibition) and also in executive functions (e.g., deductive reasoning).